An occurrence of glands in the embryo of Zea Mays

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The embryo of the grasses is an ancient battle-ground. Controversies over the homology of its various parts, and over their several functions, have been waged almost continually since the last half of the seventeenth century, when Malpighi[6] first described its anatomy. Its study formed part of the basis on which Schleiden[9] and Schacht[8] concluded that plant embryos originate in the end of the pollen-tube, while the embryo-sac serves only to protect and nourish them. By its study, in part, Mirbel and Spach,[7] and Brongniart[1] were led, on the other hand, to a diametrically opposite conclusion, namely, that the embryo originates in the embryo-sac, and that only after fecundation by the pollen.

The battle has waged fiercely over the indentification of the true cotyledon. The term scutellum (little shield), merely descriptive, harks back to Gaertner,[3] in 1788. His studies on the fruits and seeds of plants were considerably colored by his investigations of the eggs of animals, and he interpreted the shield-shaped organ in the grass embryo to be analogous to the vitellus, or nutritive part, of the animal egg. Hence he referred to it as "*vitellus scutelliformis*," or, briefly, *scutellum*. That he recognized it as really homologous with the cotyledon in other families is evidenced by the term "*scutellum cotyledoneum*" which he also employed.*

The literature shows some diversity in the significance with which the term scutellum is employed. Most authors use it, as Gaertner originally did, to apply to the entire organ, but at times its meaning has been narrowed † to the outer layer of cells, or epithelium of the shield. There seems to be little warrant and small gain in this latter restriction of it use, and the practice should be discouraged.

* "Singularem hanc Vitelli speciem, proprio *Scutelli cotyledonei* nomine distinguimus." Gaertner[3] (page cxlix).

† Brown and Herron. Jour. Chem. Soc. Lond. Trans. **35** : 623. 1879.

A discussion of the various interpretations that have been given since the time of Gaertner as to the homology of its parts, would not be germane to this paper.* Goebel,[4,5] in 1895 and 1900 on the basis of Bruns's[2] work and of his own study of *Streptochaeta*, interprets it as a true cotyledon, while "the epiblast, which lies over against it, but is not present in all grasses, is an arrested leaf," and the coleoptile, or sheath of the plumule, is the third leaf. The first green leaf is the fourth leaf of the plant. Thus the view most generally held at the present time closely agrees with that put forward by Malpighi in 1675.

Questions of function have been fully as puzzling as those of structure, if not more so, and this, too, notwithstanding the opportunities for solution by the method of experiment.

As early as 1845, Schleiden[53] regarded the scutellum of the oat as an organ of absorption, and was followed in this view by Schacht[52] and Sachs.[48, 49] It was Sachs who first pointed out the fact that the embryo, in its earlier stages of development, lives as a parasite on the endosperm, and we owe to him the term "absorptive epithelium," as applied to the outer layer of cells of the scutellum.

Three principal regions are concerned in the nourishing of the germinating embryo. These are the scutellar epithelium, the aleurone layer, and the remaining cells of the endosperm.

Dutrochet had shown that starch, as such, could not pass through semi-permeable membranes, like the cell-walls of plants, by osmosis, and thus the conclusion was forced that the food stored in the endosperm must be transformed before it could become available to the awakened embryo.

The earliest idea to develop in this connection was that the effective agent in this transformation was gluten. Fabroni, in 1785, is said † to have isolated from grape-juice a gluten-like, adhesive matter, without which fermentation did not take place. Thenard,† experimenting with several fruits, confirmed Fabroni's experiment, and considered the glutinous matter, isolated by filtering fruit juices, as identical with yeast. Thus the attention of chemists and physiologists was naturally directed to gluten as indicated above.

* The different theories have been discussed by Van Tieghem.[10, 11, 12]

† Cited by Thomson[55] (1818), page 291.

In the same year (1785), Irvine[30] pointed out the fact that, in malting, not only did the malt become sweet, but the endosperm of crushed seeds, when mixed with the malt, also became converted into sugar.

Further advance seemed to await the discovery, by Colin and Claubry,[19] in 1814, that starch is colored blue by iodine.* This discovery became a great aid in endosperm studies.

In the following year Kirchhoff,[31, 32] on the basis of his experiments, concluded that the gluten accomplishes the formation of sugar in germinating seeds, and in farina that has been scalded with hot water. He also stated that the gluten attains through germination the property of transforming into sugar a much greater quantity of starch than is to be found in the seeds, and further clearly saw that the production of sugar in germinating seeds is a chemical process, and not a consequence of vegetation.

Experiments of a similar nature to those of Kirchhoff led Thomson,[55] in 1818, to the extreme view that the essential constituent of yeast is "a species of gluten," and "that it is some substance connected with the gluten that acts upon the starch, and converts it into sugar.

The studies of Proust[43] and of Saussure,[50] in 1819, and of Dombasle,[20] in 1820, on the conversion of starch to sugar by the action of gluten, contributed only slightly to the solution of the real question, but thirteen years later, in 1833, Biot and Persoz[13] announced the discovery of dextrine, which they had produced from starch by the influence of acids.† Vogel,[58] by similar means, had, in 1812, produced what was probably the same substance, but its name and the recognition of its true nature must be attributed to Biot and Persoz.

Previous to this, Braconnot,[15] in 1824, isolated a "special principle" which changed to sugar the starch from tubers of *Helianthus tuberosus*, and in the same year in which dextrine was discovered, Saussure[51] isolated from wheat endosperm a substance similar to Braconnot's "special principle," and which alone could

* Scholz (Jour. für Chem. und Phys. **12**: 349. 1814. Footnote) attributes this discovery to Stromeyer, but gives no citation.

† Raspail,[46] who discovered the mark, or "hilum" on starch-grains, stated his belief in 1826, that "the carbonic-acid of the air is sufficient to effect the transformation of starch to sugar" (page 335).

convert into sugar four times its weight of starch. These studies, and that of Payen,[35] in 1824, paved the way for the discovery of diastase by Payen and Persoz[38] in 1833. This substance, its discoverers announced, could convert into dextrine 2,000 times its own weight of starch.

Later (1843, 1846) Payen[36, 37] demonstrated that starch must be altered "by water and diastase" before it can pass through cell-walls, and that only after being thus altered can it pass from tissue to tissue. The question now became, What is the source of the diastase by which, in germination, the endosperm is digested?

Raspail[45] had shown, in 1825, that, in germination, the endosperm gradually lost its starch, while the enlarging embryo became gradually enriched with starch-grains, and, in 1862, Sachs[48] observed that, in the germination of grass-embryos, the change of starch to sugar "begins on the side of the endosperm which lies next to the absorbing scutellum." He also demonstrated that the products of the solution of the endosperm are translocated to the germ, and homologized the scutellar epithelium "with the organ of the same name on the cotyledons of palms, and with the young epidermis of the *Ricinus* cotyledon . . . ."

From this time on, beginning with Bloziszewski,[14] in 1875, there have followed a number of researches on the germination of grass embryos deprived of endosperm, and on the ability of isolated embryos to utilize artificial endosperm. Among the earlier and more extensive of these investigations, are those of Brown and Morris,[16, 17] who demonstrated in 1888 the possibility of growing grass embryos on artificial endosperm, and, in 1890, showed that, at the beginning of germination, starch first reappears in the cells of the scutellum immediately under the epithelium. Its first appearance here, being coincident with the earliest stages of the depletion of the endosperm, was taken as evidence that it came from the latter.

The fundamental investigations as to whether or not the diastase could diffuse through cell-walls and, therefore, would not necessarily have to be secreted by the cells where it is to act, was not made until 1894, when Grüss,[23] with results contrary to those of Krabbe,[33] in 1890, demonstrated the possibility of such diffusion.

The work of Grüss indicated that the statement of Brown and Morris (1890), "that the disappearance of the cell-wall always precedes any visible attack upon the contained starch granules," is not true in all cases.

It would lead too far afield to review in detail the subsequent literature upon this topic. Experimental researches have led to at least five different views as to the place of origin of the digestive ferment during the germination of grasses. They may be briefly summarized as follows:

1. *The cells of the aleurone layer chiefly secrete the diastase,* which acts on the starch in the endosperm. This is the statement, in a more modern terminology, of the old view that starch is turned to sugar by gluten. It was tacitly assumed by Tschirch,[57] in 1889 (page 181, legend of *f. 63*).*

2. *The epithelium of the scutellum is the principal secreting layer.* This is the view of Brown and Morris,[16] in 1890,† of Grüss,[22] in 1893 (page 291), and, by implication, of Reed,[47] in 1904. According to Brown and Morris, a diastase that dissolves cell-walls is also secreted by these cells.

3. *The endosperm is the main source of the ferment,* according to Green[21] (1890), Krabbe[33] (1890), and Linz[34] (1896). "The diastase," says Krabbe, "is generally not translocated, but develops directly at the place of its activity." Secretion by the endosperm results "in consequence of some kind of stimulus on the part of the seedling." This last assertion was contradicted by Pfeffer[39] in 1893. Linz[34] definitely states (page 301), "that the epithelium of the scutellum of the seed of maize is not in a condition to secrete ferment, [and] that the epithelium is rather an apparatus which serves for the absorption of dissolved nutriment." Further on (page 318) he says, "The aleurone layer is not the source of the diastase which appears in the endosperm during germination."

4. *The scutellum and the endosperm secrete diastase,* but not so

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* The notion that pure gluten can change starch to sugar is now, of course, demonstrably erroneous, but whether or not the cells of the gluten- or aleurone-layer in the grass-fruit can secrete a diastatic ferment is a different question.

† Brown and Escombe[18] (page 14) demonstrate the hydrolytic capacity of aleurone-cells of barley, the capacity of this layer for endosperm-depletion, and that such capacity on the part of the endosperm-cells is very probable.

the aleurone layer. This view is stated by Pfeffer,[40] in 1900, (page 599), who calls the diastase secreted by the scutellum "accessory diastase," and says its secretion may always be regulated by the needs of the plant. This conclusion is based in part upon the experimental demonstration that isolated bits of endosperm placed in contact with water become spontaneously depleted. In these experiments, the disappearance of the starch proceeds centripetally from the surface of the endosperm in contact with the water.

5. *All storage tissues are capable of auto-depletion*, according to Puriewitsch.[44] This conclusion was based upon studies of the endosperm and cotyledons of various seeds, and the contents of roots, bulbs, rhizomes, tubers, and other stems. In 1896 Grüss[25] states that "It is well known that the endosperm cells themselves secrete a ferment during germination" (pages 408, 422). This, together with his paper of 1895, indicates that his position then should be classed here, but in 1897 (page 664) he says: "Seedlings from which one has taken the endosperm may, without the aid of bacteria, nourish themselves upon starch paste, which thereby becomes changed to sugar." This, however, does not necessarily imply a change from his preceding position.

In addition to the above views, may be mentioned that of Wigand,[59] who in 1888, attributed a diastatic function to the aleurone layer, but only through the mediation of bacteria developing in it; and Hansteen's,[29] founded upon extensive though insufficiently guarded experiments, that it is not necessary for diastase to proceed from the scutellum during germination.

In 1890, Haberlandt[26] stated (page 48) that "The aleurone layer of the grass-endosperm, and presumably also of seeds of other plants, is henceforth to be classed with the digestive glands of insectivorous plants," and in 1904 he states (page 477) that "its histological structure, in connection with the experimental fact that the isolated gluten layer richly secretes diastase, forms the ground for my notion concerning the function of that layer." It is interesting to note that, in this last mentioned work, the pendulum has swung back to the original idea, advanced by Kirchhoff ninety years previously, that in germinating seeds the gluten is a source of the agent that changes starch to sugar. It hardly seems probable that Haberlandt's view will finally stand.

The work of Brown and Morris indicates that the endosperm of the grass fruit is dead, but the only inference warranted by the papers of Green, Krabbe, Hansteen, Pfeffer, and Linz is, as Linz definitely states (page 312), that it is alive.

The most obvious conclusion to be drawn from this review of the literature is that there is still need for further careful experimental investigation of the subject, in which every precaution shall be used to exclude bacterial contamination, and other sources of error. Such work has been done with the date seed by Pond,[42] whose experiments seem to leave little doubt that the date-endosperm, at least, is incapable of self-digestion.*

The facts of teratology have frequently thrown light upon normal structure, helping to establish the homology of an organ whose interpretation would otherwise remain in doubt. From the fact that structure is an expression of function, anatomical variations in the direction of a structure whose rôle is well understood, may quite justifiably be taken, in connection, of course, with other facts, as evidence of the probable function of the part that varies. It was with considerable interest, therefore, in the light of our present knowledge of the homology and physiology of the parts of the fruit of the *Gramineae*, that the writer, in an examination of cross-sections of the corn grain, observed a variation in the scutellar epithelium, the significance of which can scarcely be questioned.

This tissue, one cell thick, and variously called the "absorptive epithelium" and the "glandular epithelium," is, as is well known, clearly defined anatomically from the adjacent tissue on either side. The shape of its cells, narrow and oblong in section, their palisade arrangement, and the appearance of the protoplasm, granular and relatively dense in the resting seed, more vacuolated as germination begins, and with a well defined, vigorous nucleus, clearly distinguish it. Normally it forms an unbroken layer over the convex surface of the scutellum.

In the sections examined, this layer was found invaginated in places, in such a way as to form small pockets or sacs in the tissue of the scutellum. On one side there were two such structures, and on the other side one, with a slight suggestion of an unfinished

* A conclusion contrary to that reached by the same author[41] in 1904, when there was failure to observe certain necessary precautions of method.

fourth. The diagram (FIGURE 1), shows the location of these structures in the scutellum, while they are shown in detail in the photomicrographs, FIGURES 2 and 3. Two of them, as may be seen in the diagram, are of practically uniform diameter throughout, while the other and larger one is enlarged at the end.

Describing the scutellum of the corn in 1902, Torrey[56] says: "At the region of the tip this secretory epithelial layer dips down at frequent intervals into the scutellum. The convolutions so produced secure a larger surface of secretion where there is greatest need for the enzyme; for the endosperm is thickest at this point and in front of the embryo." Whether the structures seen by Torrey were the same as those described above is not entirely clear from his description, but his figure (*f. 1*) indicates that they were at least very similar. If so, their location is not restricted "to the region of the tip" of the scutellum, as is clearly shown in

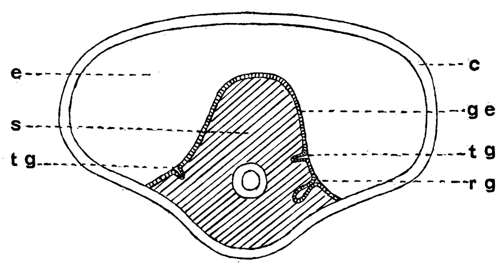

FIG. 1. Diagram of cross-section of grain of *Zea Mays*. *c*, combined coats of fruit and seed; *e*, endosperm region; *s*, scutellum; *ge*, glardular epithelium; *tg*, tubular glands; *rg*, gland slightly racemose.

FIGURE 1 herewith. Thus their distribution does not seem to be correlated with the thickness of the endosperm.

What is their significance? The variety of the corn is the "Hickory King," of J. M. Thorburn & Co., and the grains are of uniformly large area, though relatively flat and thin. Because of these facts it may be suggested, not unreasonably, that this invagination of the epithelium is merely an expression of vigorous, rapid growth, without corresponding opportunity for expansion. An analogy is found in the uneven, crinkled surface of foliage-leaves in many plants, due to the fact that one epithelium has grown more rapidly than the other. The wrinkling is a "mechan-

ical necessity." This suggestion, I think, may be dismissed at once as having too little warrant in the facts, and as being less probable than another.

If the scutellar epithelium is primarily an organ for the absorption of nutriment, as Sachs held, the variation described would be even more surprising, for we should reasonably expect an evagination, or haustorial-like projection of the tissue into the endosperm, rather than an invagination, especially if the conception of the intimate relation between structure and function is valid.

If, however, we have to deal here with an epithelium whose chief function is secretion, then the variation described is one that might

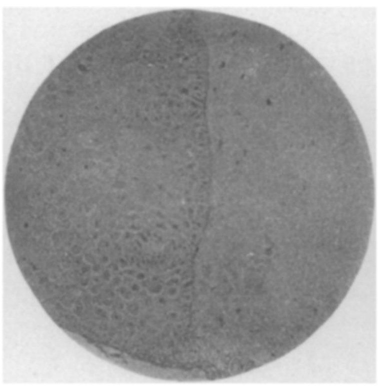

FIGURE 2

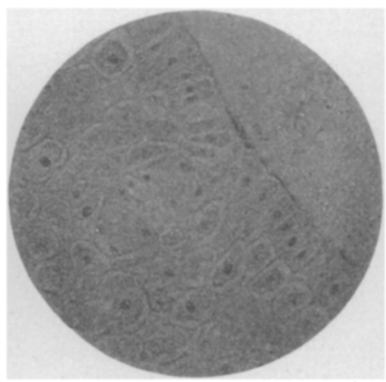

FIGURE 3

FIG. 2. Photomicrograph of cross-section of grain of maize. Tissue of scutellum at left, tissue of endosperm at right. Showing two glands in the scutellum.

FIG. 3. Photomicrograph of the upper gland of FIGURE 2, more highly magnified

have been predicted, and when once seen, the greater surprise would be that it was not of more frequent occurence. The first impression, that the anomalous structures are glands, is only strengthened by more careful observation and more thoughtful consideration. Any anatomist would at once classify the smaller invaginations as tubular glands, the simplest secreting structure next to the glandular epithelium, while the larger sac more nearly resembles a simple racemose gland.

Evidence of secretory activity was not sufficient in any part of the sections to throw light on the function of these structures. Their function may be inferred only from their anatomy, in the light of other well-known physiological observations.

Obviously no inference may be drawn from this anomaly as to the normal or the possible functions of the endosperm cells, nor of the cells of the aleurone layer, nor may any definite conclusion be drawn, on this basis alone, as to the proper function of the tissue involved. The weight of the evidence, however, is in line with all the facts of anatomy and experimental physiology which indicate that the scutellar epithelium of the grass embryo is an organ of secretion, a true glandular epithelium.

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